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1 Mass, nitrogen content, and decomposition of woody debris in forest stands affected by
2 excreta deposited in nesting colonies of Great Cormorant

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24 **Abstract**

25 Great Cormorant (*Phalacrocorax carbo*), a piscivorous bird, has established breeding
26 colonies in a coniferous forest near Lake Biwa in central Japan. This study investigated the
27 possible effects of the colony's excreta on the mass, nitrogen (N) content, and decomposition
28 of woody debris. Study plots were established in forest stands representing four stages from
29 breeding colony establishment to post-abandonment. The mass of fallen branches (diameter
30 1–5 cm) and coarse woody debris (logs, snags, and stumps; diameter ≥ 10 cm) was greater in
31 forest stands colonized by Cormorants than a control stand never colonized by Cormorants.
32 This was primarily attributed to Cormorant activity that caused increased mortality of
33 standing trees and by Cormorants breaking branches for nesting materials. Nitrogen content
34 of branches and logs that had fallen to the forest floor was negatively correlated with the
35 relative density of wood. Nitrogen content of branches was consistently higher (at a given
36 value of relative density) in the colonized stands than in the control stand. The increase of
37 branch N content was possibly caused by the incorporation of N into decomposing branches
38 with excreta-derived N supplied as throughfall and/or soil solution. The mean value of 2-year
39 mass loss of recently dead branches and logs was significantly greater for woody debris in the
40 smallest diameter class but was not significantly different among the forest stands. This
41 suggests that the excessive supply of excreta-derived N and concomitant enrichment of N in
42 soil had negligible effects on the initial stages of decomposition of woody debris.

43

44 **Keywords**

45 *Chamaecyparis obtusa* • Coarse woody debris • Decomposition • Exogenous nitrogen •

46 *Phalacrocorax carbo*

47

48 **Introduction**

49

50 Woody debris forms a dominant component of forest biomass and plays major roles in carbon
51 (C) and nutrient cycling in forest soils (Harmon et al. 1986; Stokland et al. 2012). Woody
52 debris characteristically has low nutrient content (Holub et al. 2001; Laiho and Prescott 2004)
53 and high levels of cell wall polymers such as lignin and holocellulose (Eriksson et al. 1990);
54 therefore, woody debris typically only slowly loses mass (Mackensen et al. 2001; Weedon et
55 al. 2009). Woody debris can serve as a long-term reservoir of C as well as other nutrients such
56 as nitrogen (N); colonization by decomposers and the decay decomposers induce causes
57 woody debris to slowly accumulate N (Laiho and Prescott 2004; Fukasawa et al. 2009).
58 Previous studies have produced varying results regarding how the decomposition of wood is
59 affected by the addition of exogenous N, such as through fertilization and simulated
60 atmospheric N deposition. That is, N addition can stimulate or retard the decomposition of
61 woody debris (Fog 1988; Hobbie 2008; Allison et al. 2009; Bebber et al. 2011). This suggests
62 that negative or positive feedback may occur when N is plentiful in terms of the sequestration
63 of C and N in woody debris.

64 The population of Great Cormorant (*Phalacrocorax carbo* Kuroda), a piscivorous
65 bird, has increased in size from 1992 to 2001 alongside Lake Biwa in central Japan (Ishida et
66 al. 2003; Kameda et al. 2003). Cormorants feed on fish in the lake (Takahashi et al. 2006) and
67 drop excreta in breeding colonies established in nearby forest stands, thus transferring N from
68 aquatic to terrestrial ecosystems (Kameda et al. 2006). Nesting Cormorants break off branches
69 and leaves in local forest stands of *Chamaecyparis obtusa* Endl. for nesting material, and

70 often drop them on the forest floor. This results in a 7–22 times greater input of litterfall (2.6
71 Mg ha⁻¹ month⁻¹ on mean) during the breeding season than occurs naturally in control forest
72 stands (Hobara et al. 2001). In addition, the Cormorants excrete large amounts of N in their
73 feces, increasing the N input by about 10,000 times that ordinarily received from precipitation
74 (Kameda et al. 2000). This excessive supply of N has been shown to influence the species
75 composition and physiological capabilities of decomposer fungi (Osono et al. 2002, 2006b). It
76 also retards decomposition and enhances the immobilization of N in decomposing needles
77 and twigs with diameters less than 5 mm (Osono et al. 2006a). These changes lead to changes
78 in N cycling in the forest floor and mineral soils (Hobara et al. 2001, 2005). Fujiwara and
79 Takayanagi (2001) documented increased tree mortality at sites with the greatest avian impact
80 causing trees to exhibit symptoms of forest decline. In contrast, few studies have examined
81 the mass, N content, and decomposition of woody debris [classified here as (1) branches and
82 (2) coarse woody debris (CWD)] in forest stands that are receiving an excess supply of N of
83 avian origin. We thus hypothesized that the colonization of forest stands by Great Cormorants
84 and concomitant supply of excessive excreta-derived N (i) results in an increase in the mass
85 and N content of CWD and (ii) retards the decomposition of woody debris on the forest floor.

86 The purpose of the present study was to investigate the possible effects of avian
87 colonization and excreta deposition on mass, N content, and mass loss rates of woody debris
88 of *C. obtusa* in a temperate evergreen coniferous forest. First, we compared the mass and N
89 content of woody debris consisting of both branches (diameter 1–5 cm) and CWD (logs,
90 snags, and stumps; diameter \geq 10 cm), among four forest stands that had very similar
91 vegetation composition but were in different stages of breeding colony establishment. We
92 then compared the 2-year mass loss of recently-dead woody debris in three diameter classes

93 (1, 3, and 10 cm) among the forest stands to demonstrate whether Cormorant colonization and
94 excreta deposition affected the initial stages of decomposition on the forest floor.

95

96 **Materials and Methods**

97

98 Study site

99

100 The study was carried out at a 57 ha site known as the Isaki Headland (90 to 210 m a.s.l.;
101 35°12'N, 136°5'E), on the southeast side of Lake Biwa, Ohmihachiman City, Shiga Prefecture,
102 Japan. The Hikone Weather Station reported a mean annual temperature of 14.6°C and annual
103 precipitation of 1591.9 mm about 20 km northeast of the site from 1980 to 2005. The
104 dominant tree species on the Isaki Headland was *Chamaecyparis obtusa* Sieb. et Zucc.
105 (Fujiwara and Takayanagi 2001).

106 The population of Great Cormorant along Lake Biwa increased from about 3,000
107 birds in 1992 to about 16,450 in 2001 (Ishida et al. 2003). A colony of Cormorants was first
108 discovered in the Isaki Headland in 1988, and the number of nests increased from 30–40 in
109 1989 to 5,300 in 1999 (Fujiwara and Takayanagi 2001).

110 Four study sites on Isaki Headland, coded as Sites NC (never colonized), AC (active
111 colony during study; Cormorants abundant), A1 (abandoned after three years; no Cormorants
112 in 2003–2005), and A2 (declined in 1997 to 2002 after 4 years of intensive colonization; no
113 Cormorants in 2003–2005), had very similar vegetation composition but were in different
114 stages of breeding colony establishment, use, and abandonment by the Cormorants (Table 1).
115 Cormorants intensively colonized site AC and the birds were estimated to drop 2.2 Mg ha⁻¹

116 month⁻¹ of excreta during the breeding season; this was estimated to be the equivalent of 240
117 kg ha⁻¹ month⁻¹ of excreta-derived N (Kameda et al. 2000).

118

119 Census of CWD and branches

120

121 In the present study, we established a single very long 2030 m × 4 m belt transect that
122 included the four sites. We divided the belt transect into 202 grids (10 m × 4 m), and each of
123 the 202 grids was allocated to Sites NC, AC, A1, or A2 and used for the measurement of
124 CWD. CWD included logs (diameter ≥ 10 cm at the base), snags (height ≥ 120 cm, diameter
125 ≥ 10 cm at breast height), and stumps (height < 120 cm, diameter ≥ 10 cm at the base). A total
126 of 661 logs, snags, and stumps were marked in 2003, and each of them was assigned to one of
127 the four tree species based on the remaining bark, branching characteristics, and/or the degree
128 of bend of stem, when available. Each piece of CWD was also assigned to one of the five
129 decay classes [least (I) to most decayed (V)] using visual criteria provided by Fukasawa et al.
130 (2014). The volume of logs and snags was estimated using the method described in Fukasawa
131 et al. (2014), and that of stumps was calculated from the height and diameter, with stumps
132 considered to be cylinders.

133 One to ten CWD items were then chosen for each tree species, each form, and each
134 decay class, and wood samples were collected using an electric drill to estimate the relative
135 density of each piece of tested CWD. A drill bit (length 24 cm, diameter 9 mm) was used to
136 drill into the CWD from the outer surface to the center; one to three drill holes were made per
137 log, depending on log size, and all wood particles removed by drilling were harvested. The
138 depth of each drill hole was measured. For well-decayed logs that were too fragile to be

139 drilled, pieces of wood were collected and whittled into a rectangular parallelepiped to
140 estimate wood volume. The samples were returned to the laboratory, oven-dried to constant
141 weight at 40°C and weighed. The relative density (g cm^{-3}) of samples was then calculated as
142 the dry weight divided by the volume of the drill hole or wood block. The mass of CWD was
143 then calculated by multiplying the volume and the relative density measured for each category
144 of debris.

145 We also established nine 1×1 m quadrats at each site and adjacent to the belt
146 transect. The quadrats were used for the collection of branches and the decomposition
147 experiment described below. We randomly chose five of the nine quadrats at each site and
148 used them to describe the mass of branches (diameter 1 to 5 cm at the base) at Sites AC, A1,
149 and NC. A total of 767 branch samples were collected in 2003, oven-dried at 40°C to a
150 constant mass, and weighed. Each branch was assigned to one of the three tree species using
151 the method described above. Each branch was then assigned to one of the three decay classes
152 as defined above. Branches in decay class I had bark and intact wood; those in decay class II
153 had loose bark and slightly rotten wood; and those in decay class III had detached bark and
154 rotten wood.

155

156 Nitrogen content of woody debris

157

158 Samples of logs and branches of *C. obtusa* collected from the forest floor were used for N
159 analysis. These included 74 logs (12 to 24 logs per site) in various decay classes and 90
160 branches ($2 \text{ branches} \times 3 \text{ decay classes} \times 5 \text{ quadrats} \times 3 \text{ sites}$). The oven-dried samples were
161 ground in a laboratory mill and passed through a 0.5-mm screen. Total N content (mg g^{-1} dry

162 litter) was measured by automatic gas chromatography (NC analyzer SUMIGRAPH NC-900,
163 Sumitomo Chemical Co., Osaka, Japan).

164

165 Mass loss rate of woody debris

166

167 Decomposition of woody debris was studied with 2-years of field incubation experiments.

168 Wood samples in three diameter classes were prepared in May 2003 from a *C. obtusa* tree cut

169 in a forest stand never affected by the Cormorants. These included 72 wood samples 1 cm in

170 diameter and 4 cm long (D1), 72 samples 3 cm in diameter and 40 cm long (D3), and 12

171 samples 10 cm in diameter and 90 cm long (D10). Wood sub-samples were collected from

172 D10 samples using an electric drill, three holes per sample, as described above, to calculate

173 the relative density (g cm^{-3}) of the samples.

174 The decomposition study covered a 24-month period from June 2003 to June 2005.

175 In June 2003, D1 and D3 samples were placed on the litter layer of nine quadrats at each site

176 and tethered with metal wire to prevent movement. D10 samples were placed on the litter

177 layer of three quadrats randomly chosen for each site. Sampling of these samples took place

178 twice, at one (June 2004) and two years (June 2005) after the placement. On each sampling

179 occasion, one D1 and one D3 sample was retrieved from each quadrat, making a total of 72

180 samples ($9 \text{ quadrats} \times 4 \text{ sites} \times 2 \text{ collections}$) for each of D1 and D3. Wood sub-samples were

181 collected from D10 samples only in June 2005 (after two years) using an electric drill as

182 described above. D1 and D3 samples and the sub-sampled D10 wood particles were

183 oven-dried to constant weight at 40°C and weighed, and the relative density of the D10

184 sub-samples was calculated as described above. The losses of dry mass (D1 and D3) and

185 relative density (D10) were determined (as % of the original mass), and mean values of mass
186 loss were calculated for each sampling and each site.

187

188 Statistical analyses

189

190 When comparing the N content of logs and branches between the study sites with different
191 stages of Cormorant colonization, the effect of relative density of wood on the N content
192 needs to be taken into account, because N content of woody residues generally increases with
193 the loss of relative density during decomposition (Fukasawa et al. 2009, 2012, 2014).
194 Therefore, linear relationships between the relative density and N content were examined for
195 each study site according to the following equations:

196

$$197 \quad \text{N content} = a + b \times (\text{relative density}). \quad (1)$$

198

199 Intercepts (a) and slopes (b) of regression equations were calculated for the linear
200 relationships using least-squares regression. Analysis of covariance (ANCOVA) was then
201 used to evaluate the differences in regression equations among the study sites. The
202 significance of the homogeneity of the slopes was evaluated, and when no significance was
203 found, the interaction term was excluded from the analysis (Sokal and Rohlf 1995). When
204 slope b differed between study sites, the regression with the greater b value showed a smaller
205 decrease in the dependent variable y with respect to the unit increment of the independent
206 variable x . This indicated a significant difference existed between the rates of changes in N
207 content versus relative density. When b did not differ between study sites, but the intercept a

208 differed, the regression with the larger a value had a consistently greater y value at any given
209 x value, indicating a significant difference in N content at given values of relative density
210 between the study sites. The generalized linear model (GLM) was used to evaluate the
211 difference in 1- and 2-year mass loss of woody debris using diameter class, study site, and the
212 interaction of diameter class \times study site as independent variables. These analyses were
213 performed with JMP 6.0 software for Macintosh.

214

215 **Results**

216

217 **Mass of CWD and branches**

218

219 The mass of CWD ranged from 7.72 to 42.05 Mg ha⁻¹ and was greater at Sites AC, A1, and
220 A2 than at Site NC (Table 2). *Pinus densiflora* accounted for 62.6% of CWD mass at Site NC
221 and this was attributed to a previous outbreak of pine wilt disease; however, *C. obtusa* was a
222 major component at Sites AC, A1, and A2 (32.6 to 74.4%). Snags were major components of
223 CWD at Sites AC, A1, and A2 (67.5 to 87.4%). CWD in the decay class I was the dominant
224 component at Site AC but its proportion decreased to Site A1 and again to Site A2, whereas
225 the proportion of CWD in the decay class II increased as the age of the Cormorant colony
226 increased from Sites AC to A1 to A2.

227 The mass of branches was greater at Sites AC and A1 than at Site NC (Table 2).

228 Branches of *C. obtuse* in the decay class II were the dominant component at these three sites.

229

230 **Nitrogen content**

231

232 N content of logs and branches on the forest floor ranged from 0.33 to 7.13 mg g⁻¹ and from
233 1.15 to 11.38 mg g⁻¹, respectively (Fig. 1). The linear relationships between N content and
234 relative density were statistically significant for all sites (logs: $R = -0.59$ to -0.70 , $P < 0.05$;
235 branches: $R = -0.81$ to -0.85 , $P < 0.001$), indicating that the N content of decomposing logs
236 and branches increased as their relative density decreased (Fig. 1). Neither the slope nor the
237 intercept of the regression equation for logs was significantly different among the study sites
238 (ANCOVA, slope: $F = 1.23$, $P = 0.31$; intercept: $F = 0.30$, $P = 0.83$). The slope of the
239 regression equation for branches was not significantly different among the sites (ANCOVA, F
240 $= 1.75$, $P = 0.19$). Furthermore, the intercept of N content was significantly different in the
241 order: Site AC > Site A1 > Site NC (ANCOVA, $F = 51.5$, $P < 0.001$), indicating that the N
242 content of branches was consistently higher at Sites AC and A1 than at Site NC at a given
243 value of relative density.

244

245 Mass loss

246

247 Mean values of mass loss of woody debris ranged from 1.2 to 9.9% for the first year and from
248 6.6 to 25.1% for the second year (Fig. 2). The 1-year mass loss was significantly affected by
249 diameter class (GLM, deviance = 531.2, $P < 0.001$) but not by study site (GLM, deviance =
250 54.7, $P = 0.20$) or by the interaction of diameter class \times study site (GLM, deviance = 25.9, P
251 $= 0.53$). The same result was found for the 2-year mass loss; that is, the mass loss was
252 significantly affected by diameter class (GLM, deviance = 2195.0, $P < 0.001$) but not by
253 study site (GLM, deviance = 155.4, $P = 0.57$) or by the interaction of diameter class \times study

254 site (GLM, deviance = 518.4, $P = 0.34$). The mass loss was greatest for woody debris in the
255 smallest diameter class.

256

257 **Discussion**

258

259 The mass of CWD at Site NC (control, never known to be colonized by Cormorants) in the
260 present study (Table 2) was within the range previously reported for temperate coniferous
261 forests (Siitonen et al. 2000; Ranius et al. 2003). However, those at the historic or present
262 colony sites, Sites AC, A1, and A2, were at the upper end of or beyond the previous range,
263 indicating that the activity of Cormorants caused increased mortality of standing trees
264 (Fujiwara and Takayanagi 2001). Standing trees were being actively converted to snags in the
265 decay class I in the forest stand presently colonized by Cormorants (Site AC) and then
266 decomposed gradually to decay class II after the birds abandoned the colony and the forest
267 stand declined (Table 2). Similarly, the Cormorants' active removal of branches for nesting
268 materials, some of which they accidentally dropped, (Fujiwara and Takayanagi 2001), led to
269 the greater mass of branches on the forest floor at Sites AC, A1, and A2 than at Site NC
270 (Table 2).

271 The N content of branches (diameter 1 to 5 cm) was higher in the order: Site AC >
272 Site A1 > Site NC, regardless of their relative density, whereas similar differences among the
273 study sites were not found for logs (diameter more than 10 cm; Fig. 1). Osono et al. (2006a)
274 also found increased N content in decomposing twig litter (diameter less than 5 mm) at Site
275 AC, which was the result of immobilization of excreta-derived N. Thus, the results of the
276 present study demonstrated that the smaller woody debris served as a better N reservoir than

277 the larger debris on a time scale of at least 7 years of Cormorant colonization (Table 1). The
278 higher N content in branches in forest stands presently and previously colonized by
279 Cormorants was probably caused by the incorporation of excreta-derived N into the branches.
280 Excreta-derived N may be readily supplied to branch decomposers as ammonium ions in
281 throughfall solution (Osono et al. 2006b) and/or ammonium ions and nitrates in soil solutions
282 (Hobara et al. 2001), and became immobilized in decomposing branches at Sites AC and A1.
283 The lack of N increase in log samples in the present study may be caused by their low surface
284 area to volume ratio when compared to that of branches and/or the use of bulk samples for N
285 analysis that included not only surface wood tissues but also inner tissues that had been less
286 decomposed.

287 By combining the data of amount of branches on the forest floor at Sites AC, A1,
288 and NC (Table 2) and the increased N content in branches at Sites AC and A1 relative to Site
289 NC (Fig. 1), we were able to calculate a stand-level accumulation of N in fallen branches and
290 its contribution to the total amount of N deposited as excreta. For each Site, specifically Sites
291 AC, A1, and NC, we multiplied the mean values of N content of *C. obtusa* branches in three
292 decay classes by the total weight of branches in these decay classes (kg ha^{-1} ; Table 2). The
293 total N amount in branches was found to be 15.96 kg ha^{-1} at Site AC, 13.76 kg ha^{-1} at Site A1,
294 and 3.14 kg ha^{-1} at Site NC. Hence, Sites AC and A1 had 12.83 and 10.62 kg ha^{-1} more N
295 found in branches relative to Site NC, respectively. These values of the amount of N found in
296 branches accounted for 5.3% and 4.4% at Sites AC and A1, respectively, of monthly N input
297 as excreta during the breeding season at Site AC ($240 \text{ kg ha}^{-1} \text{ month}^{-1}$; Kameda et al. 2000).
298 This calculation is obviously tentative but implies the low contribution of N incorporated into
299 branches to the total input of excreta-derived N. Similarly, Osono et al. (2006a) suggested

300 needles and twigs of *C. obtusa* had a potential to immobilize only 7% of total excreta-derived
301 N deposited on the forest floor at Site AC. Hobara et al. (2005) also reached the same
302 conclusion, stating that the increased pool size of N in surface soil (forest floor plus mineral
303 soil) at Site AC compared with Site NC was less than the amount of N transported by
304 Cormorants. Leaching into deeper soil layers served as the major pathway of excreta-derived
305 N cycling through the forest system (Hobara et al. 2005).

306 The 2-year decomposition field experiment showed that the mass loss of woody
307 debris was not significantly different among forest stands that differed in their history of
308 Cormorant colonization (Fig. 2). This finding suggests that the excessive supply of
309 excreta-derived nutrients at Site AC and the concomitant enrichment in soil of nutrients at
310 Site A1 had negligible effects on the initial stages of decomposition of woody debris. The
311 mass loss rates found here were within the range reported for conifer woody debris in
312 temperate regions (Brown et al. 1996; Frangi et al. 1997; Hyvönen et al. 2000; Inagaki and
313 Fukata 2003). The low surface area to volume ratio of woody debris (Harmon et al. 1986)
314 may partly account for the insensitivity of initial wood decomposition to Cormorant
315 colonization. In contrast, Osono et al. (2006a) found slower mass loss of fine litter (needles
316 and twigs less than 5 mm in diameter) of *C. obtusa* at Site AC than at Site NC, which was
317 attributed to the reduction in lignin decomposition by fungal colonizers (Osono et al. 2006b;
318 Osono 2007).

319 The present study demonstrates that (i) the mass of CWD and branches increased
320 and (ii) the branch N content increased in forest stands presently and previously colonized by
321 Cormorants, and that (iii) Cormorant colonization had no significant effects on the 2-year
322 mass loss of woody debris. Further long-term studies are needed to evaluate the effects of

323 excreta deposition on the decomposition of CWD (larger than 10 cm in diameter) and the
324 roles of CWD as a long-term reservoir of C and N in Cormorant-colonized forests. CWD was
325 four to six times more abundant than branches in the present study sites (Table 2), and more
326 importantly, most CWD was present as snags in the colonized forests and persisted as
327 standing-dead snags for 10 years after Cormorant colonization (e.g., at Site A2); of course,
328 this gradually shifted to more advanced decay classes (Table 2). Particular attention should be
329 paid to the rates of fragmentation of these snags to fallen logs and the processes of
330 decomposition and N dynamics of these logs; this will allow us to better understand C and N
331 accumulation and turnover in CWD in forest stands affected by the excreta of Cormorants.

332

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341

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426

427 Figure legends

428

429 **Fig. 1** Relationship between nitrogen content and relative density of (a) logs and (b) branches
430 of *Chamaecyparis obtusa* on the forest floor of Sites NC, AC, A1, and A2 at different stages
431 of Cormorant colonization. Logs and branches had diameters ≥ 10 cm and 1 to 5 cm,
432 respectively. Squares and a black line indicate Site NC; gray circles and a gray line, site AC;
433 black triangles and a broken line, site A1; black diamonds and a dotted line, site A2. No data
434 were available for branches at Site A2. Analysis of covariance (ANCOVA) was then used to
435 evaluate the differences in the regression equations among the study sites. *** $P < 0.001$, ns,
436 not significant.

437

438 **Fig. 2** One- (a) and 2-year (b) mass loss (% original mass) of woody debris of *Chamaecyparis*
439 *obtusa* of three diameter classes incubated on the forest floor of the four sites (Sites NC, AC,
440 A1, and A2) at different stages of Cormorant colonization. D1, 1 cm diameter; D3, 3 cm
441 diameter; D10, 10 cm diameter. Values indicate means \pm standard errors. No data were
442 available for the first-year mass loss of D10. A generalized linear model (GLM) was used to
443 evaluate the difference in 1- and 2-year mass loss of woody debris using diameter class, study
444 site, and the interaction of diameter class \times study site as independent variables. *** $P < 0.001$,
445 ns, not significant.

Fig. 1

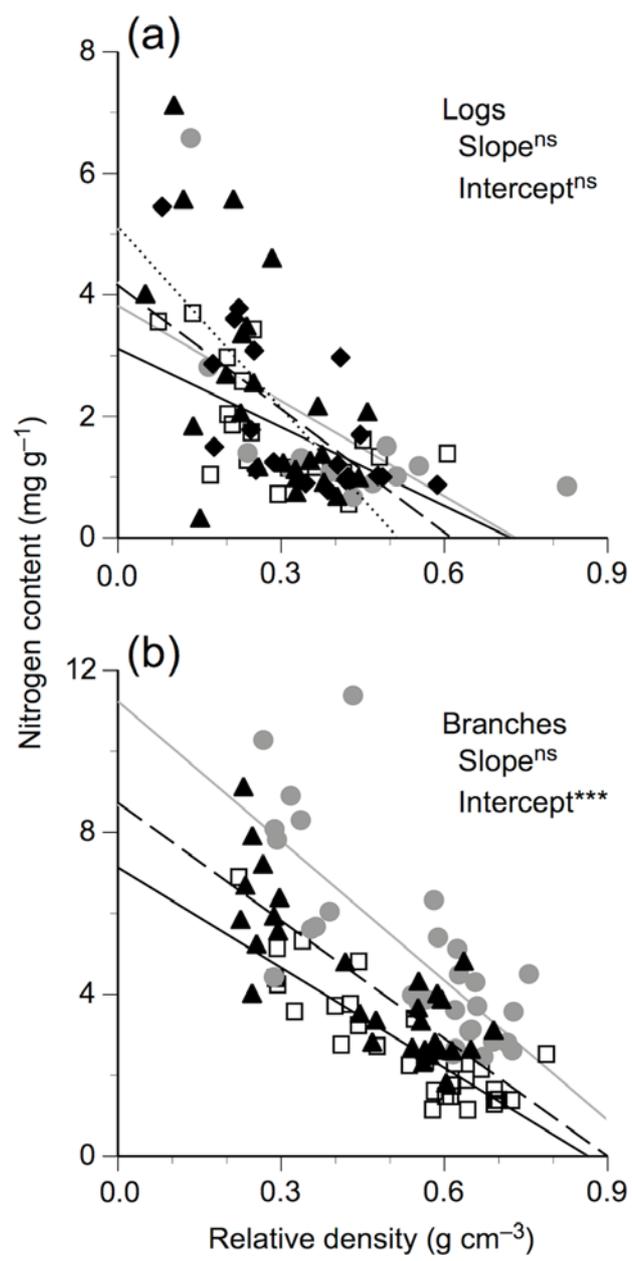


Fig. 2

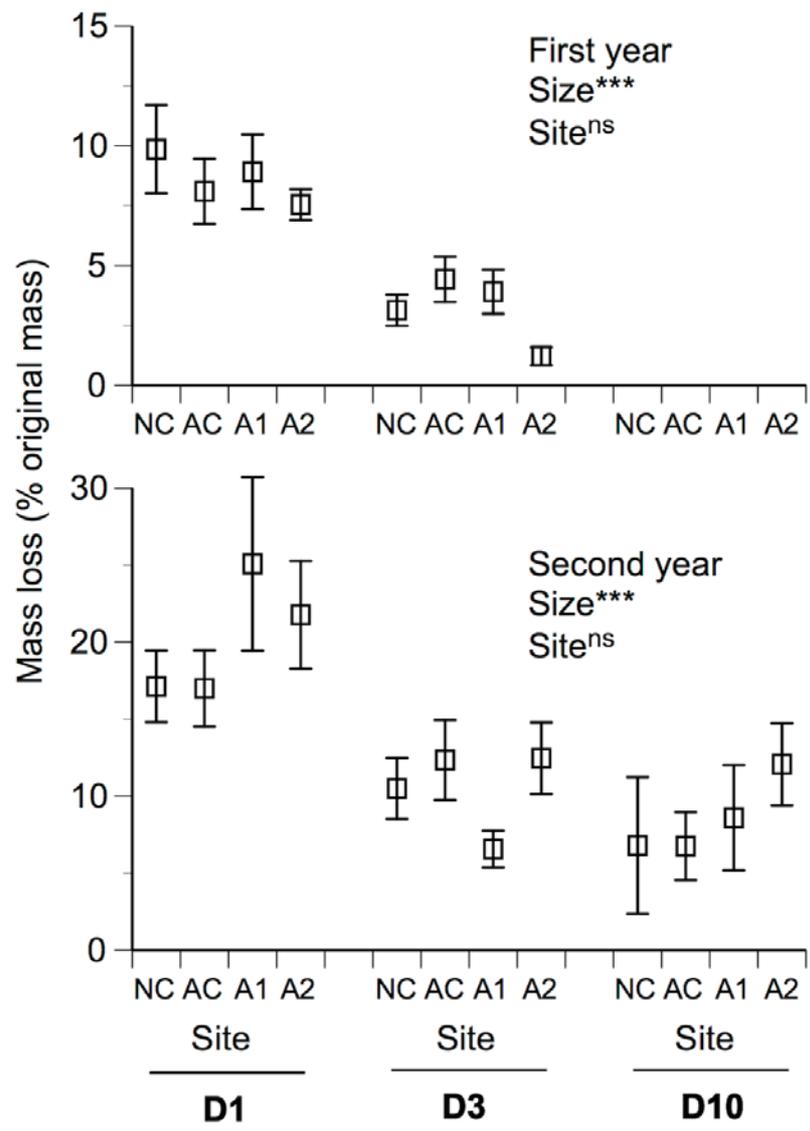


Table 1 Study sites and descriptions of Cormorant breeding colonies (Fujiwara and Takayanagi 2001; Kameda et al. 2006).

Site	Colonization period	Description
NC	No colonization	Never known to be colonized by Cormorants (control)
AC	1997–2005	Active colony during study; Cormorants abundant
A1	1996–1999	Abandoned after 3 years of colonization; no Cormorants in 2003–2005
A2	1992–1996	Declined in 1997 to 2002 after 4 years of intensive colonization; no Cormorants in 2003–2005

Sites NC, AC, A1, and A2 correspond to sites C, 1, 2, and 3, respectively, in Osono et al. (2006a, 2006b).

Table 2. Mass (Mg ha^{-1}) and compositions of coarse woody debris (CWD; diameter ≥ 10 cm) and branches (diameter 1–5 cm) in four forest stands (Sites NC, AC, A1 and A2 of Table 1). Numbers in parentheses indicate the proportions relative to the total mass. Measurement of branches was not performed at Site A2. nd, not determined. Cypress, *Chamaecyparis obtusa*; pine, *Pinus densiflora*.

	NC		AC		A1		A2	
	Coarse woody debris							
Total	7.72	(100.0)	25.28	(100.0)	15.54	(100.0)	42.05	(100.0)
Tree species								
Cypress	1.78	(23.1)	16.21	(64.1)	5.07	(32.6)	31.31	(74.4)
Pine	4.83	(62.6)	7.27	(28.8)	4.66	(30.0)	2.72	(6.5)
Broad-leaved	0.95	(12.4)	1.67	(6.6)	4.07	(26.2)	6.93	(16.5)
Unknown	0.16	(2.0)	0.13	(0.5)	1.73	(11.1)	1.10	(2.6)
Form								
Log	2.85	(37.0)	6.05	(23.9)	4.04	(26.0)	3.90	(9.3)
Snag	3.30	(42.7)	17.38	(68.7)	10.49	(67.5)	36.77	(87.4)
Stump	1.57	(20.3)	1.86	(7.3)	1.00	(6.4)	1.38	(3.3)
Decay class ^a								
I	2.69	(34.8)	17.54	(69.4)	7.95	(51.2)	5.30	(12.6)
II	2.13	(27.5)	0.27	(1.1)	6.13	(39.5)	30.47	(72.4)
III	1.65	(21.4)	1.72	(6.8)	0.67	(4.3)	5.05	(12.0)
IV	1.23	(15.9)	5.68	(22.4)	0.78	(5.0)	1.24	(3.0)
V	0.03	(0.4)	0.08	(0.3)	0.00	(0.0)	0.00	(0.0)
	Branch							
Total	1.27	(100.0)	3.85	(100.0)	3.59	(100.0)	nd	Nd
Tree species								
Cypress	0.99	(78.1)	2.24	(58.1)	3.10	(86.4)	nd	nd
Pine	0.00	(0.0)	0.79	(20.4)	0.00	(0.0)	nd	nd
Broad-leaved	0.28	(21.9)	0.83	(21.5)	0.49	(13.6)	nd	nd
Decay class ^b								
I	0.17	(13.7)	0.78	(20.3)	0.47	(13.0)	nd	nd
II	0.81	(64.0)	2.86	(74.1)	2.33	(64.9)	nd	nd
III	0.28	(22.3)	0.22	(5.6)	0.79	(22.1)	nd	nd

^a Decay class of CWD followed Fukasawa et al. (2014). Decay class I, bark is intact, structural integrity sound, small twigs present, invading root absent; decay class II, bark is mostly intact, sapwood somewhat decayed, larger twigs present, invading roots absent; decay class III, bark is sloughing or absent, heart wood mostly sound and supports own weight, large branches present, invading roots present only in sapwood; decay class IV, bark is detached or absent, heart wood rotten and does not support own weight, branch stub present,

invading roots throughout; decay class V, bark is detached or absent, no structural integrity, branches absent, invading roots throughout.

^b Branches in decay class I had bark and intact wood; those in decay class II had loose bark and slightly rotten wood; and those in decay class III had detached bark and rotten wood.